

# FIRST RECORD OF FOOTPRINTS OF TERRESTRIAL VERTEBRATES FROM THE UPPER PERMIAN OF THE CIS-URALS, RUSSIA

by VALENTIN P. TVERDOKHLEBOV, GALINA I. TVERDOKHLEBOVA,  
MICHAEL J. BENTON *and* GLENN W. STORRS

**ABSTRACT.** The first tetrapod footprints from the Upper Permian of Russia are identified as *Anthichnium* ichnosp., on the basis of a short track from the Severodvinskian Gorizont (upper Tatarian, uppermost Permian) of Kulchomovo, 75 km east-north-east of Orenburg, southern Pre-Urals basin. The footprints are preserved in a ripple-marked sandstone unit, and appear to show an animal swimming, then crawling through wet marginal sediment, and finally moving on to firmer substrate. The sedimentary setting is an enclosed semi-arid foreland basin, close to high mountains. An ephemeral stream-playa lake complex developed, with long emergent periods and short episodes of flooding and stream development. The footprints were probably produced by a small temnospondyl amphibian with four fingers and five toes.

MORE than 1000 occurrences of terrestrial vertebrates are known from the Upper Permian and Triassic continental red beds of the easternmost European part of Russia (Efremov and Vjushkov 1955; Olson 1957; Tverdokhlebova 1976; Ochev *et al.* 1979). Tetrapod remains have been found in virtually all areas where such strata occur, from the Barents Sea in the far north, well within the Arctic Circle, to the Pre-Caspian region in the south (Text-fig. 1). However, vertebrate tracks have not hitherto been found in this vast territory, and we make the first report here of such an occurrence.

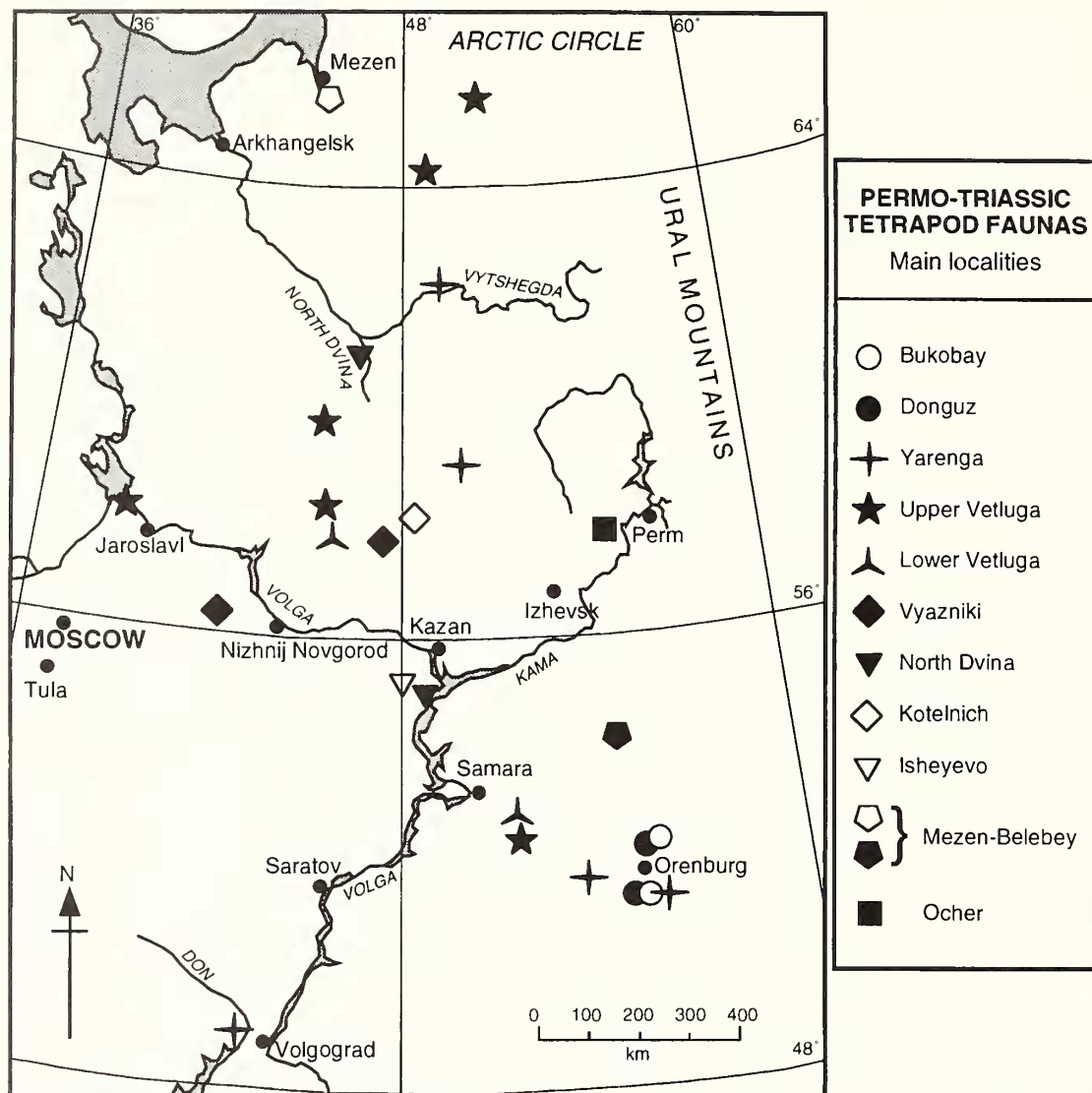
The footprints, dated as Tatarian (Upper Permian), are small, and the track is preserved on a series of seven adjoining blocks that are easily transported and pieced together. These are housed in the collection of the Scientific Research Institute of Geology, Saratov State University, SGU No. 104 B/2060-2065. Four additional and adjacent blocks without tracks are also preserved.

## GEOLOGICAL SETTING

### *Locality and age*

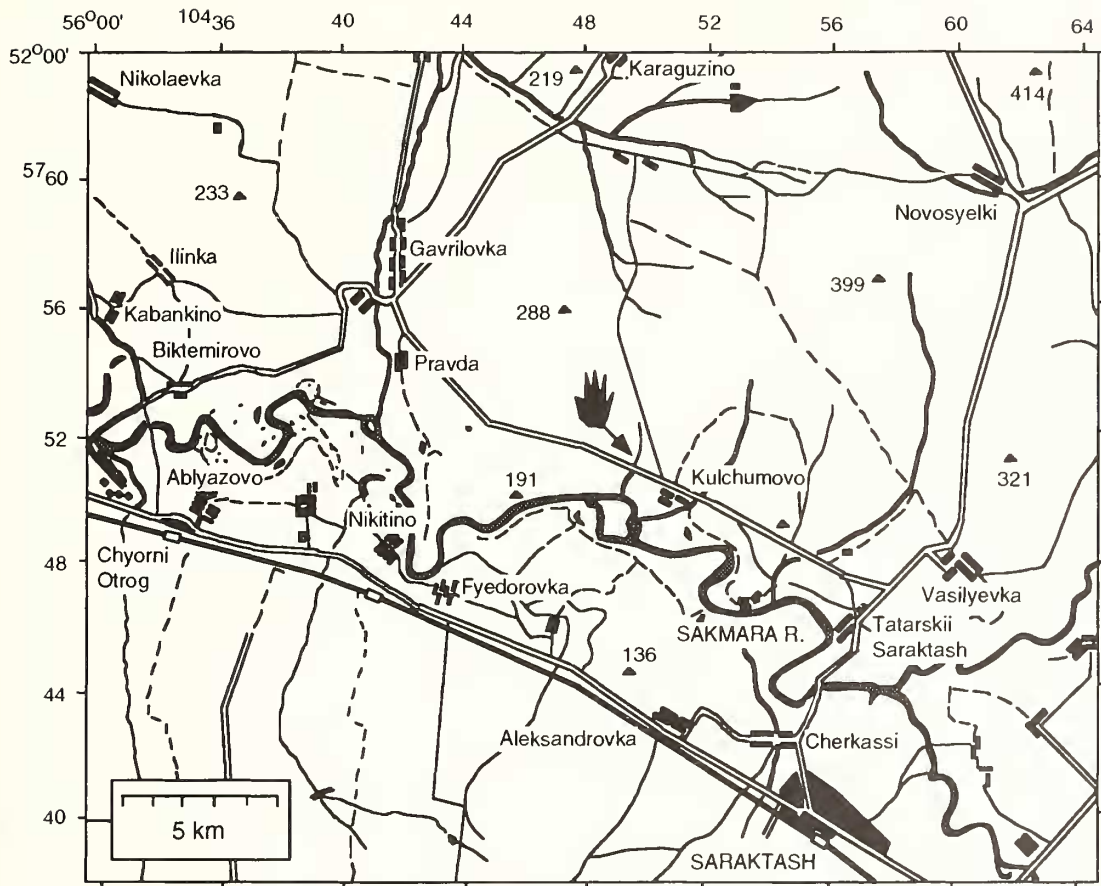
The footprints were found in 1988 by one of us (VPT) in the southern Cis-Uralian (Pre-Ural) Trough close to the right bank of the Sakmara river, 75 km east-north-east of the city of Orenburg (Text-fig. 1). The locality lies just to the north of a graded dirt road ('graida') on the west bank of a small unnamed stream (Text-fig. 2), about 12 km north-west of Saraktash. The 'graida' runs east-south-east from the village of Gavrilovka and crosses the stream in question after about 10.5 km, and about 1.5 km before the road passes the tiny settlement of Kulchumovo. The map reference for the locality, using the Soviet 'Sistema Koordinat 1942' is  $104^{\circ}49'25.7''$  E,  $51^{\circ}53'$  N.

The sedimentary rocks exposed in the stream section belong to the Severodvinskian (North Dvina) Gorizont ('horizon'), of late Tatarian (latest Permian) age. This unit is a widespread, and widely recognized, biostratigraphical division in both the Ural and Povolzhye (near-Volga) regions (Anfimov *et al.* 1993). A Russian gorizont is not equivalent to a lithostratigraphical horizon of western nomenclature, but rather is defined solely on the basis of its contained fauna and flora. The Severodvinskian is characterized especially by the ostracod *Suchonellina futschiki*. It has yielded also



TEXT-FIG. 1. Map of major Permo-Triassic tetrapod localities on the Russian Platform and in the Cis-Uralian Trough. The specimens described herein are from near Orenburg, in the south-east.

the bivalves *Palaeomutela orthodonta*, *P. ovalis*, and *Sacmariella novovulvhumica*, the gastropods *Vethugaia aristovens* and *V. suchonensis*, the conchostracans *Pseudestheria plotnikovi* and *Sphaerestheria belorussica*, and the ostracods *Darwinula inornata*, *D. inornata* var. *macra*, and *D. parallela* (Anfimov *et al.* 1993). Associated vertebrate fossils include skeletons of temnospondyls (*Dvinosaurus egregius*, *D. primus*), anthracosaurs (*Bystrowiana permira*, *Chroniosaurus dongusensis*, *Jugosuchus boreus*, *J. hartmanni*, *Raphanodon tverdokhlebovae*), pareiasaurs (*Deltavjatka vjatkensis*, *Scutosaurus permianus*, *S. itilensis*, *S. rossicus*), dicynodonts (*Dicynodon trautscholdi*), gorgonopsians (*Proburnetia vjatkensis*, *Sauroctonus progressus*) and therocephalians (*Moschowhaitzia vjuschkovi*, *Niuksenitia suchonensis*) (Tverdokhlebova 1976).



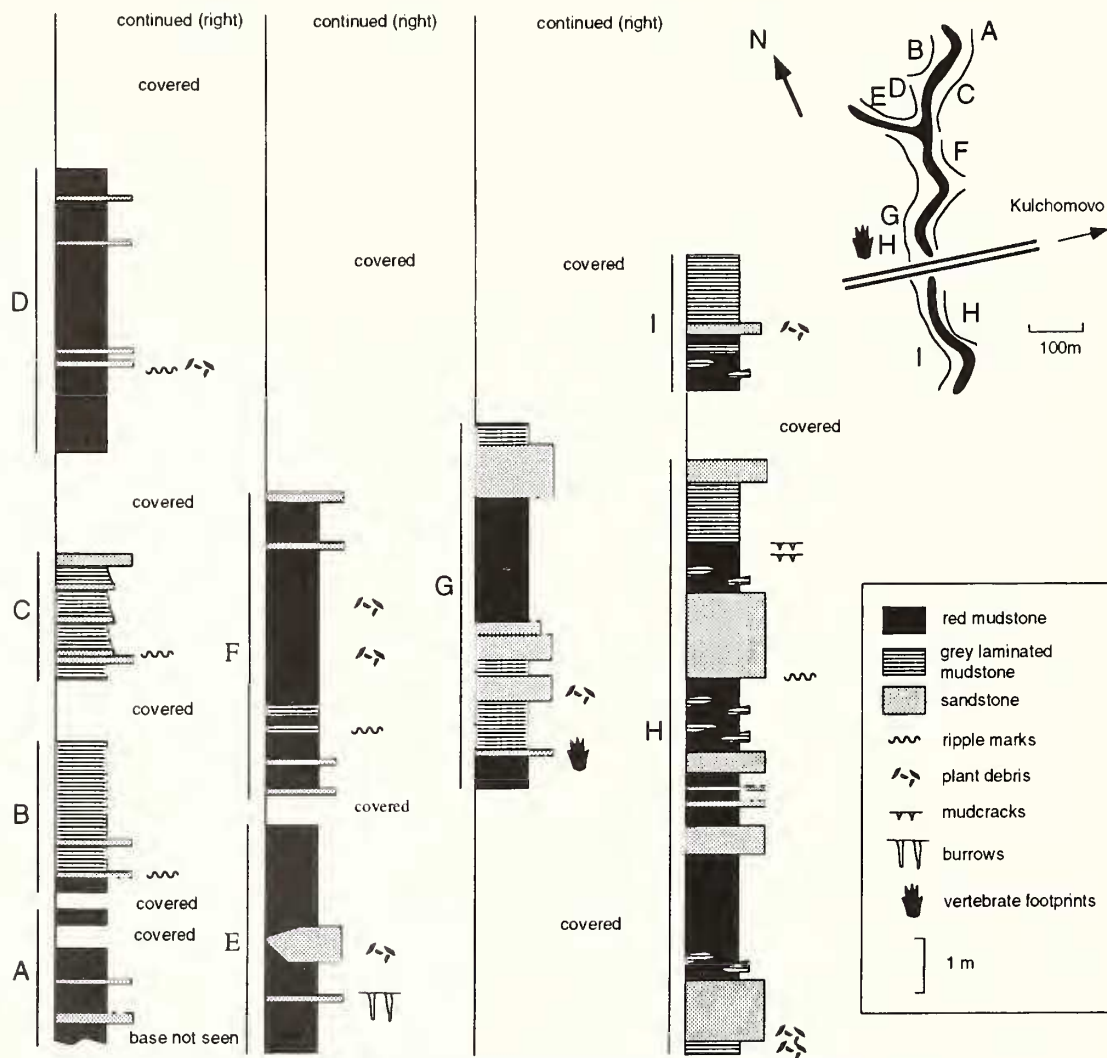
TEXT-FIG. 2. Detailed locality map for Kulchumovo tetrapod trackway (location indicated by footprint outline).

The Severodvinskian Gorizont is the lower of two biostratigraphical divisions forming the Upper Tatarian Substage, the higher one being the Vyatskian Gorizont. Below the Severodvinskian, the Urzhumskian Gorizont corresponds to the entirety of the Lower Tatarian Substage. In general, the biostratigraphical divisions of the Upper Permian in Russia, and especially the Tatarian, are based upon fossil tetrapod data (Efremov and Vjushkov 1955; Tverdokhlebova 1976), although recent studies of ostracods have produced good section correlations (Molostovskaya 1982, 1993). The utility of bivalves and conchostracans is as yet limited. It may be noted here that Kozur (1993) has placed the Cis-Uralian Tatarian rather earlier than latest Permian.

Cis-Uralian rocks belonging to the Severodvinskian are seen particularly in the north-west part of the Perm region, some 600 km north of Orenburg. Around Perm, they consist mainly of limestones, some of which are dolomitized, and marls. Some of the limestones show evidence of algal/stromatolitic origins. East and south of Orenburg, Severodvinskian rocks consist of cyclic sequences of alternating mudstones, siltstones, and flaggy sandstones, with bedded clays, limestones, and conglomerates (Garyainov *et al.* 1967, p. 4). The lithostratigraphical unit of the Kulchumovo locality is unnamed locally, but may be equivalent to the Severodvinskian Malokinelsk Svita of the Russian Platform. A Russian svita is the nearest lithostratigraphical equivalent to a western formation, although the definitions of such svitas are less formal.

*Sedimentology*

The footprints were found on the surface of a light-grey fine-grained calcareous sandstone, which is laterally discontinuous, and up to 0.05 m thick. The sandstone unit is one of many in a sequence (Text-fig. 3) of mudstones and sandstones, in which mudstones make up about 90 per cent. of the



TEXT-FIG. 3. Logged stratigraphical section along unnamed stream bed near Kulchomovo containing tetrapod trackway. The locations of parts of the logged section are shown in the sketch-map at top right.

thickness of the succession. Some of the thin sandstone beds extend laterally for 10 m or more, but there are some obvious channels, such as at point E in the logged section (Text-fig. 3). The succession consists of 70 m or more of mudstones, siltstones, and sandstones, showing ripple-cross-laminated sets 0.2 m thick. The sandstones are grey-buff; the mudstones may be grey or red. The mudstones are all laminated to some extent, but the lamination is clearest in the grey mudstones.



Fossils in these units consist of carbonized vegetation and feeding burrows of invertebrates, as well as conchostracans, ostracods, bivalves and macerated fish remains.

The sandstone slabs which bear the tracks vary in thickness, being thinnest towards the bottom. They are grey, of very fine sand or silt grade and are only slightly laminated, almost massive. A carbonate cement binds the grains. They are considered to have been deposited subaqueously, as indicated by the nature of the tracks and associated sedimentary structures (see below). The slabs bear current ripple marks on their top surfaces. These ripples are lobate and semi-crescentic with sharp asymmetrical crests, up to *c.* 8 mm high. Flow direction was from top to bottom, as illustrated. Ripple cross-laminations occur also, on a scale of 50–80 mm long and 12–20 mm high. Obvious rain-marks are seen all over the upper surface of the slabs, clearly developed on ripple crests, but much less distinct or absent in the ripple troughs. All have indistinct borders. One slab shows four successive rain-print levels in cross section. The surface troughs between ripples show evidence of having been filled with rain water, which later drained away and/or evaporated, leaving successive, finely defined, concentric tide marks. The slabs lay at the top of a unit of red mudstones. On the under surface of the footprint-bearing sandstones there are impressions of crescentic ripples, desiccation cracks and rain-drop prints, cast from the underlying unit. The desiccation cracks are 1.5–2.0 mm deep.

## SYSTEMATIC PALAEOLOGY

Genus *ANTHICHNIUM* Nopcsa, 1923

*Anthichnium* ichnosp. indet

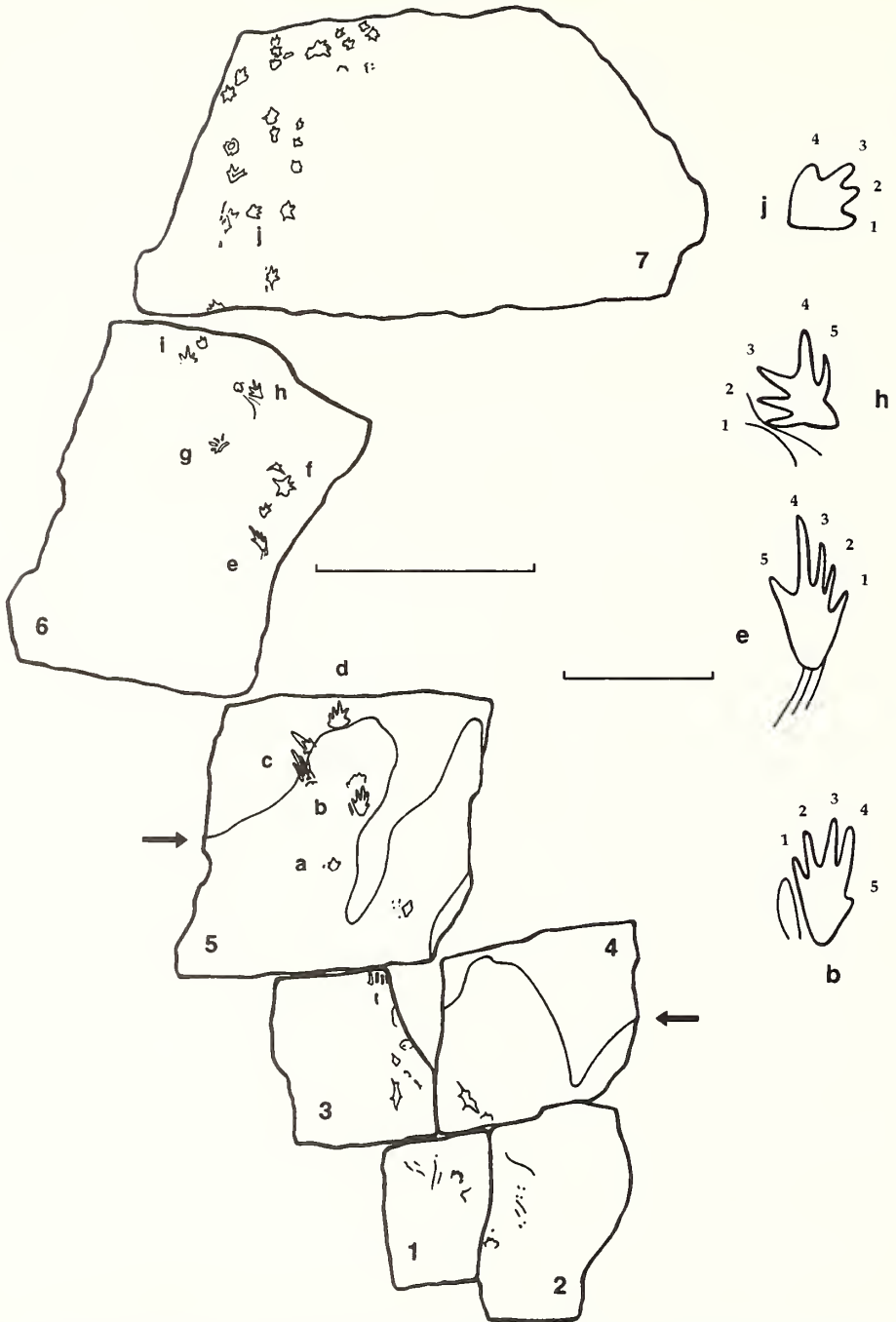
Text-figure 4

### *Description*

The tracks are those of a small (approximately 100 mm long), sprawling, quadruped. The prints are generally indistinct, but the overall pattern of sinuous movement is clear. The track proceeds from the bottom to the top of the specimen as figured (Text-fig. 4). The first marks, on slabs 1–4 (Text-fig. 4), are in the form of furrows made by claws and traces of pads, seemingly produced by a floating animal whose feet barely touched bottom. However, these marks are very distinct since they were imprinted on a fine carbonate mud film overlying the typical sand. Farther up the track (slabs 3, 5), where the animal stepped with its full weight on the bottom, traces left by its longer hind limbs are evident (e.g. Text-fig. 4, print a). These have rather smooth and rounded edges, presumably since the sediment near the water's edge was oversaturated or even covered with water. In this region, however, there are distinct rain-drop imprints on the landward side of the ripple crests (slabs 4–5). The 'land' was wet fine-grained sand arranged in cusped ripple marks, with small pools of water lying in the depressions between ripples.

After passing out of the water-saturated littoral zone on to firmer substrate (slabs 5–7), the footprints become better defined, and the toe marks are clearly seen, some terminating in pointed claw marks. Near the top of slab 5, the animal climbed the stoss side of a ripple, and three clear footprints are preserved on the crest (Text-fig. 4, prints c–d). It is interesting that the leftmost two of these prints (c) appear to represent the same foot, a second successful attempt to climb the ripple following an initial slip of the left foot (print c) from the muddy ripple crest. Print d lies on the downstream edge of the crest and the heel impression is not preserved. Above that site, on slabs 6 and 7, the animal followed a flatter route, and produced more regular tracks (prints e–i, Text-fig. 4). Print 6e (Text-fig. 4) exhibits short slippage marks behind the heel. Prints f–h have more splayed toes in somewhat deeper mud; a ridge of mud has been pressed up by the step forming print 6h (Text-fig. 4). A similar extruded mud crest lies to the right of the middle (right hind) print of slab 5 (print b, Text-fig. 4). The track swings to the right near the top of slab 7 along the line of the ripple crests.

Most of the footprints are incomplete, having washed-away or water-worn edges. The best preserved hindprints, on block 6 (Text-fig. 4), measure approximately 8 mm wide × 10 mm long. Their five toes are much longer and more slender than the digits of the forelimbs; digit 4 is apparently the longest. The best foreprint, on slab 7 (print j, Text-fig. 4), is *c.* 6 × 6 mm and shows only four short and stubby digits, number 3 being the longest. None of the other less well preserved foreprints shows more than four digits. The smoothed, slipping, footprints in the 'shoreline' region (slabs 4 and 5) are 5–7 mm long, and 1.5–2.0 mm deep. The spacing between opposite limbs was 25–30 mm, based on measurements of maximum track width. The traces left by fore and hindlimbs generally occur close together, or even overlap, with the hind occasionally stepping in and



TEXT-FIG. 4. Schematic interpretation of assembled tetrapod trackway slabs, *Anthichnium* ichnosp. (SGU No. 104 B/2060-2065), from the late Tatarian, Severodvinskian Gorizont, near Kulchumovo, Orenburg Oblast, Russia, and detail of four of the prints. Waterline indicated by arrows. Scale bars represent 100 mm (main slab), and 10 mm (individual prints b, e, h, j).

obliterating the foreprint, and is typical for the trackway of a quadrupedal sprawler. Stride length varies enormously within this short segment of trackway, as the animal's progress was variously impeded by slick substrate conditions and topographical obstacles. For instance, the strong ripples of block 7 interfered with the creature's movement and significantly shortened its stride. The stride length appears most uniform and normal on the relatively high, hard ground of slab 6 (Text-fig. 4). Here it may also be measured most readily, where three clear impressions of the left hindlimb (e, g, i) are spaced, heel to heel, 47 mm (e to g) and 41 mm (g to i) apart. Two imprints of the right hindlimb (f, h), also on slab 6, indicate a heel to heel stride length of 46 mm. The foreprints lie on average 4–6 mm in front of the hindprints on block 6.

#### *Identification of the trackmaker*

Comparison with previously described footprints suggests one of three tetrapod groups as trackmaker: amphibians, procolophonids, and diapsids, all of which are well known from the Upper Permian. Of these, the procolophonids and diapsids generally had five fingers and five toes, and footprints ascribed to those two groups (such as *Paluichnus* or *Phalalgichnus*, and *Anthonoichnium* respectively) are too large for comparison (Haubold 1971, pp. 31, 43–44). Small amphibian footprints, such as *Anthichnium* and *Batrachichnus*, on the other hand, are comparable. Individual prints of these taxa are generally 10 mm, or less, in length, the foot has longer digits than the hand, there are four fingers and five toes, and the foot is plantigrade (Haubold 1971, pp. 13–14). Both have generally been reported only from the Upper Carboniferous and Lower Permian (Haubold 1971; Fichter 1983), but excellent tracks identified as *Anthichnium* have been reported from the Upper Permian of Provence, France (Demathieu *et al.* 1992; Gand *et al.* 1995). These show all the features noted above, as well as the relative lengths of the toes, which match those seen in the Russian specimen (b, e, Text-fig. 4). Gand *et al.* (1995) classify *Anthichnium* in the temnospondyl family Branchiosauridae, but that assignment is not certain.

Among amphibians from the Severodvinskian Gorizont of the Cis-Urals area, the anthracosaurs *Chroniosaurus* and *Raphanodon* were small enough to be the trackmaker. The digit counts and phalangeal formulae of these forms are unknown, but it is unlikely that they would have had four manual digits. Temnospondyls, on the other hand, had four digits. The temnospondyls from the Severodvinskian Gorizont of the Cis-Uralian area, species of *Dviuosaurus*, were too large in comparison with the tracks. However, juvenile *Dviuosaurus*, or an as yet unknown adult temnospondyl species, was probably responsible.

## DISCUSSION

#### *Sedimentary environment*

The sedimentary succession exposed at the trackway locality near Kulchumovo appears to represent a marginal lake environment, probably of ephemeral nature, in the broad shallow basins to the west of the ancestral Urals. The mix of grey and red mudstones with minor fine-grained calcareous sandstones, many of them laterally continuous, the associated ripple marks, rain-drop impressions, desiccation cracks, disseminated plant debris, and vertebrate tracks are all typical features of such environments (Picard and High 1972). The trackway slabs represent a narrow zone close to the edge of a pool or lake, into which rainwaters flowed periodically, creating the lobate, asymmetrical ripples.

The setting is similar to that of the Late Permian Lower Beaufort Group of the Karoo Basin, South Africa, the environment of deposition of which is interpreted (Stear 1983) as an ancient ephemeral stream–playa lake complex that formed in a semi-arid inland basin. Sheet-like and lenticular sandstone bodies occur as superimposed systems of fluvial channels and overbank splays, with abundant evidence for falling water levels and emergence. Stear (1983) interpreted the Lower Beaufort Group sediments as largely high-energy clastic materials washed into a semi-arid basin from seasonal rainfall or glacial meltwaters in surrounding upland areas. These periodic short-term inundations incised deep channels, and waters ran to the middle of the basin where there was a



shallow lake or playa. The water seeped into the ground or evaporated during the rest of the year, when rainfall or glacial runoff was minimal, and emergent features, such as desiccation cracks, evaporites, and calcretes, developed during these times. The Pre-Ural basin shares all of these sedimentological features, and its tectonic setting (foreland basin) is also the same as the South African example. Fine- and coarse-grained sediment transported from arid plains into lakes that lack any drainage route present highly favourable conditions for preservation of surface sedimentary structures and footprints.

The Kulchumovo sediments, however, indicate a hot, semi-arid climate with intense seasonality. There is no evidence locally for dramatic rainfall which would have produced sudden flooding events, forming deep wadi-like channels. If such wadis existed, they were presumably situated more proximally, on relatively high mountain slopes. Rain showers were apparently moderate locally (although potentially torrential proximally), raising water levels periodically, and bringing silt and sand pulses into lakes and pools that normally experienced slow deposition from suspension of clays and muds. Between rain showers, there were drying phases, during which the exposed mud surfaces became cohesive. Further rainfall brought in more sediment rapidly enough to preserve surface impressions and desiccation cracks, while continuing the cycle of lake level oscillation. Tverdokhlebov (1988, 1989) has suggested that regional conditions allowed for deposition of great thicknesses of mud in a relatively short period of time, perhaps seasonally. The change at the footprint level from red to grey rocks corresponds to a locally more stable aquatic environment and reducing conditions. Fossils of aquatic organisms are more common above the horizon that yielded the tracks.

The Late Permian sequences of the Cis-Urals are interpreted (Newell *et al.* in press) as deposits of a transverse drainage system characterized by channels which decreased in size downcurrent and terminated in a muddy flood basin. The range of facies indicates a terminal fan setting. The Kulchomovo locality belongs to Newell *et al.*'s (in press) distal facies association: deposits of a muddy basin which generally received only fine-grained sediments after large floods. Occasional sheet sandstones and heterolithic channel fills are incised into the mudflats.

### *The track-bearing horizon*

The track-site sediments indicate in some detail the sequence of events. The layers of mudstone beneath the footprint-bearing sandstone were presumably deposited subaqueously; then the lake dried, exposing and cracking the mud. Several closely spaced showers of rain brought sheetfloods of sand across the cohesive dry mud surface, creating ripples and laminae. The rain continued after the sand had been deposited, showering the sand surface, and pitting the tops of the ripples. Water gathered in the hollows between ripples and formed a shallow pool lapping up on to the sand. A thin mud drape fell from suspension on to the sand.

The rain then stopped, and a small tetrapod swam to the edge of the pool, paddling itself on to the shore, and scratching the bottom as it did so. It pulled itself out of the water, and picked its way over the firmer ripple crests until it escaped from the immediate water's edge. At the beginning of the track, as preserved (Text-fig. 4), the animal was apparently swimming, as shown by the incomplete scratch marks produced by the toes contacting the sediment. As it emerged from the water, the animal crossed a narrow zone of water-saturated sand, into which it sank, leaving ill-defined prints. Then, moving on to drier sand, the trackway shows that the animal walked round a water-filled depression. Of the clear prints near the top of slab 5 (Text-fig. 4) two show impressions of a slipping foot and a hand close together, presumably because the small animal had to struggle to surmount the steep ripple facing it.

The track was produced *after* a shower of rain, as indicated by the fact that the rain imprints have not erased the footprint impressions. After the animal had passed over this narrow belt of land, the water in the ripple hollows soaked away through the sand, or evaporated in the rays of a hot sun. The whole process probably lasted little longer than 24 hours. Shortly after, the pool or lake again flooded the site, covering the footprint-bearing layer with grey mud and sand. Typical freshwater



organisms, such as conchostracans and ostracods, as well as fishes and bivalves, occupied the new lake.

*Acknowledgements.* MJB and GWS thank the Royal Society for funding their visits to Russia in the summers of 1994 and 1995, as part of the Royal Society Joint Research Programme between palaeontologists in Russia and Bristol. MJB and GWS also thank their hosts from Saratov State University, especially Professor V. G. Ochev, for their great kindness and assistance. GWS acknowledges the contribution of research facilities at the Geier Collections and Research Center, Cincinnati Museum of Natural History, and the Department of Geology, University of Cincinnati, for aiding this work. We thank Andrew Milner for helpful comments on the nature of the track-maker.

## REFERENCES

- ANFIMOV, L. V., CHUVASHOV, B. I., GRIFER, B. I., GUSEV, A. K., KOCKLIN, A. I., MURAVYEV, I. S., SOFRONITSKY, P. A. and ZOLOTOVA, V. P. 1993. General characteristics of the Permian deposits of the Urals and Povolzhye: Upper Permian. *In* Permian System: guides to ecological excursions in the Uralian type localities. *Occasional Publications, Earth Sciences and Resources Institute, University of South Carolina, Columbia, New Series*, **10**, 24–33.
- DEMATHIEU, G., GAND, G. and TOUTIN-MORIN, N. 1992. La palichnofaune des bassins permien provençaux. *Geobios*, **25**, 19–54.
- EFREMOV, I. A. and VJUSHKOV, B. P. 1955. [Catalogue of localities of Permian and Triassic terrestrial vertebrates in the territories of the U.S.S.R.]. *Trudy Paleontologicheskii Instituta*, **46**, 1–185. [In Russian].
- FICHTER, J. 1983. Tetrapodenfährten aus dem saarpfälzischen Rotliegenden;? Ober-Karbon, Unter-Perm; Südwest-Deutschland, I: Fährten der Gattungen *Saurichnites*, *Linnopus*, *Amphisauroides*, *Protritonichnites*, *Gilmoreichnus*, *Hyloidichnus* und *Jacobiichnus*. *Mainzer Geowissenschaftlichen Mitteilungen*, **12**, 9–121.
- GAND, G., DEMATHIEU, G. and BALLESTRA, F. 1995. La palichnofaune de vertébrés tétrapodes du Permien Supérieur de l'Estérel (Provence, France). *Palaeontographica, Abteilung A*, **235**, 97–139.
- GARYAINOV, V. A., KULYOVA, G. V., OCHEV, V. G. and TVERDOKHLEBOV, V. P. 1967. [Guidebook to excursions through Upper Permian and Triassic continental sediments of the south-west of the Russian Platform and Pre-Urals]. Izdatelstvo Saratovskogo Universiteta, Saratov, 148 pp. [In Russian].
- HAUBOLD, H. 1971. Ichnia amphibiorum et reptiliorum fossilium. *Handbuch der Paläoherpetologie*, **18**, 1–124.
- KOZUR, H. 1993. Boundaries and subdivisions of the Permian System. *In* Contributions to Eurasian Geology. *Occasional Publications, Earth Sciences and Resources Institute, University of South Carolina, New Series*, **9B**, 139–154.
- MOLOSTOVSKAYA, I. I. 1982. [History of development of Late Permian ostracods of the subfamily Darwinulacea on the Russian Platform and their significance for regional stratigraphy]. *Voprosi Micropaleontologii*, **25**, 155–163. [In Russian].
- 1993. Nonmarine ostracods and paleobiogeographical distribution of Late Permian basins in the Eastern Russian Plate. *In* Contributions to Eurasian Geology. *Occasional Publications, Earth Sciences and Resources Institute, University of South Carolina, Columbia, New Series*, **9B**, 95–100.
- NEWELL, A. J., TVERDOKHLEBOV, V. P. and BENTON, M. J. in press. Sedimentology of late orogenic (Permian, Tatarian) molasse from the southern Ural foreland basin. *Sedimentology*.
- NOPCSA, F. 1923. Die Familien der Reptilien. *Fortschritte der Geologie und Paläontologie*, **2**, 1–210, pls 1–6.
- OCHEV, V. G., TVERDOKHLEBOVA, G. I., MINIKH, M. G. and MINIKH, A. V. 1979. [Stratigraphical and palaeogeographical importance of Upper Permian and Triassic vertebrates of the East European platform and Pre-Urals]. Izdatelstvo Saratovskogo Universiteta, Saratov, 160 pp. [In Russian].
- OLSON, E. C. 1957. Catalogue of localities of Permian and Triassic terrestrial vertebrates of the territories of the U.S.S.R. *Journal of Geology*, **65**, 196–224.
- PICARD, M. D. and HIGH, L. R., Jr 1972. Sedimentary cycles in the Green River Formation (Eocene), Uinta Basin, Utah. *Journal of Sedimentary Petrology*, **38**, 378–383.
- STEAR, W. M. 1983. Morphological characteristics of ephemeral stream channel and overbank splay sandstone bodies in the Permian Lower Beaufort Group, Karoo Basin, South Africa. 405–420. *In* COLLINSON, J. D. and LEWIN, J. (eds). *Modern and ancient fluvial systems*. International Association of Sedimentologists Special Publication, 6. Blackwells, Oxford, 527 pp.
- TVERDOKHLEBOV, V. P. 1988. [Some general problems of investigation of arid continental ecosystems]. Manuscript N 359-B 88, deposited in Saratov State University, Saratov. [In Russian].

- 1989. [Methodological aspect. Genetic types of continental sediments of the arid and semi-arid zone and taphonomic peculiarities in connection with their localities of the remains of tetrapods]. 66–73. In [*Theory and experiment in taphonomy. Materials of the scientific seminar on questions of taphonomy and paleoecology, Saratov, May 1986*]. Izdatelstvo Saratovskogo Universiteta, Saratov, 162 pp. [In Russian].
- TVERDOKHLEBOV, G. I. 1976. [*Catalogue of tetrapod localities of the Upper Permian of the southern Pre-Urals and the south-eastern Russian Platform*]. Izdatelstvo Saratovskogo Universiteta, Saratov, 88 pp. [In Russian].

VALENTIN P. TVERDOKHLEBOV

GALENA I. TVERDOKHLEBOVA

Nauchno-Issledovatel'skii Institut Geologii  
Prospekt Moskovskaya, 161  
410750 Saratov, Russia

MICHAEL J. BENTON

Department of Geology  
University of Bristol  
Bristol BS8 1RJ, UK

GLENN W. STORRS

Department of Geology  
University of Bristol  
Bristol BS8 1RJ, UK  
and

Geier Collections and Research Center  
Cincinnati Museum of Natural History  
1720 Gilbert Avenue  
Cincinnati, Ohio 45202, USA

Typescript received 22 November 1995  
Revised typescript received 27 March 1996